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WITH THE AUTHOR'S COMPLIMENTS.

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Terminology of the Spore Forms and Associated Structures of the Rust Fungi.

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TERMINOLOGY OF THE SPORE FORMS AND ASSOCIATED STRUCTURES OF THE RUST FUNGI.

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To the casual student the confusion in terminology existing in the rust fungi constitutes a very real obstacle to an intelligent understanding of the order, and an attempt at classification of the position is my apology for the presentation of this paper.

Many of the terms in use to-day for the various fruiting-structures and spores of the rusts have been evolved gradually as a result of studies extending over a period exceeding a century. In consequence several have no longer a precise application, are inconsistently applied, and often are ambiguous. The problem of terminology is rendered difficult in that no less than five spore forms and their associated structures may occur in the cycle of a single species. Thus in the well-known wheat-rust, *Puccinia*

graminis, are present the following spores and structures (which, with the exception of basidia, are termed sori) producing them :—

Sori.	Spores.
Spermogonia.	Spermatia.
Æcidia.	Æcidiospores.
Uredosori.	Uredospores.
Teleutosori.	Teleutospores.
Basidia.	Basidiospores.

The following historical *résumé* shows the manner in which most of these terms have been derived. It will be seen that many have had subsequently a different meaning or usage than when they were first proposed. This has in part contributed to confusion in their interpretation or use.

Persoon (1801) was the first to attempt classification of the rusts. He erected the genera *Aecidium*, *Uredo*, and *Puccinia* to contain the few species known at that time, for he was unaware that the two first were but stages in the cycle of the last and similar genera. To the sori he applied the name "cespitosus," and to the spores "sporulæ." Later Rebentisch (1804), Link (1809), and Leveille (1826) erected the genera *Roestelia*, *Caeoma*, and *Peridermium*, being also unaware that these were merely forms in the cycles of species belonging to genera of the families Pucciniaceæ and Melampsoraceæ. Link used "sporidia" for the spores, irrespective of the structure in which they were produced.

The first progressive step towards a concise terminology was taken by the brothers Tulasne (1847), and by L. R. Tulasne (1851, 1853), who applied to Persoon's "cespitosus" the more concise "sorus," and separated the sori into two types—(*a*) "spermogonia" producing "spermatia" (because of the supposed similarity of these to the spermogonia of certain lichens), and (*b*) "fruits." The latter was subdivided according to the type of spores produced by them; thus what are now known as uredospores were termed "stylospores," and teleutospores were named "sporæ perfectiores" (perfect spores). Infection hyphæ (germ-tubes) produced by germinating æcidiospores or uredospores were termed "promycelia," and spores produced by germinating teleutospores became "sporidia."

The second progressive step was taken by De Bary (1865), following his demonstration by the aid of cultures that the "genera" *Aecidium* and *Uredo* occurred in the cycle of species (such as *Puccinia graminis*) possessing teleutospores. Prior to this these spore forms, as well as others (*Roestelia*, *Caeoma*, and *Peridermium*) were regarded as distinct genera. De Bary adapted the names "æcidium" and "uredo" from the genera erected by Persoon, and, by attaching them suitably, coined the terms "æcidiospore" and "uredospore." For the "perfect spore" of Tulasne he employed "teleutospore" (literally end spore), because it appeared at the end of the cycle (as he had just demonstrated in his cultural experiments). By employing the termination "sorus" proposed by Tulasne he coined the additional terms "uredosorus" and "teleutosorus," and used "æcidium" in a similar sense for the sorus producing æcidiospores. In a later work he used the term "basidium" for structures now known as æcidiospore initials (the structures producing and supporting the æcidiospore chains in the æcidium).

Tulasne, it will be remembered, used "promycelium" for the infection hyphæ produced by germinating æcidiospores and uredospores, and also for basidia produced by germinating teleutospores, although unaware of the true significance of the latter structures. The basidiospores were termed "sporidia"; and this term was changed to "sporidiola" by De Toni

(1888), and to "promycelial spore" by Plowright (1889). Then Brefeld (1889) demonstrated that both "promycelia" and "sporidia" were basidia and basidiospores respectively, and named them accordingly.

Van Tieghem (1893) considered the teleutospore to be a "probasidium," since it did not behave like a spore, but acted instead as "an encystment of the basidium"; and his term has by certain subsequent workers been applied either to teleutospores or basidia.

Following De Bary's use of the terms "æcidiospore" and "uredospore," derived from the names of form-genera, numerous workers attempted to define other spore forms in a similar manner, with the result that for a time such terms as "cæomatospore," "rœsteliospore," or "peridermiospore" came into more or less general use. In recent years such have been almost wholly abandoned, but have been revived in a somewhat elaborate form in a recent work published by Arthur *et al.* (1929).

P. and H. Sydow (1904) applied to the structures termed "spermogonia" and "spermatia" by Tulasne the terms "pycnidia" and "pyncidiospores," under the mistaken idea that they were structurally, or possibly functionally, similar to pycnidia and spores of certain conidial forms of the Ascomycetes. And one or two recent workers have changed the term "pycnidiospore," as used by the Sydows, to "conidia," under the mistaken idea that they function as such.

This, then, was the position when Arthur (1905) proposed that the older terms be replaced with others he coined, on the grounds that the former were "clumsy, ambiguous, poorly correlated, and quite inadequate to show homologies properly." As Arthur's terms were not defined, they were regarded merely as substitutes for the older ones, and disregarded by mycologists other than those resident in the United States. Consequently Arthur and Kern (1926) defined the terms proposed previously by Arthur, and urged their universal application. Finally Arthur *et al.* (1929) proposed (in addition to those previously coined) a new set of terms more exactly defining æcidia of different types and teleutospores of microcyclic species. These terms are listed below.

As a standard terminology is not in use, and as many of the terms are either ambiguous or erroneously applied, I suggest that standardization be attempted on the basis of the following dicta :—

(1) That the sorial nature of the fruiting-structures be indicated by the termination "sorus";
(2) That terms be applied primarily on a morphological, not a cytological or functional basis;
(3) That terminations be uniform throughout;
(4) That precedence be given to terms in general use, save where these are ambiguous or misleading;
(5) That ambiguous terms be replaced by others with a concise meaning and, where possible, a modern interpretation.

A set of standardized terms based on these dicta is given below. These require a minimum number of changes, are uniform in their application, and avoid ambiguity of interpretation, since most are self-explanatory :—

Pycniosorus (plural, pycniosori).—This is suggested in place of "spermogonium," "spermogone," "pycnidium," or "pycnium," all of which are in more or less general use. For these structures are morphologically and functionally sori, producing spores which are functional (Craigie, 1927); they are neither male conceptacles nor pycnidia. "Pycnium" is not consistent with terms in current use (as uredosorus or teleutosorus), and does not indicate the sorial nature of this structure, and therefore should be abandoned.

Pycniospore (pl., pycniospores).—This is suggested in place of "sporidium," "spermatium," "pycnidiospore," or "conidium." For these spores are neither bodies of male sex nor conidia. The term is comparable with æcidiospore or uredospore (words in current use), and is the only one accepted of those proposed by Arthur or Arthur *et al.*

Æcidiosorus (pl., æcidiosori).—This is suggested in place of "æcidium" or "æcium": Firstly, because this term indicates more clearly the sorial nature of this structure; secondly, because, as "æcidium" was derived from the form-genus of that name, its use leads to confusion when applied to æcidiosori of the *Roestelia, Peridermium*, or *Endophyllum* type; thirdly, because its use unifies the term with uredosorus or teleutosorus. Arthur's term "æcium" cannot be used, because it has been applied to æcidiosori, cæomosori, primary and secondary uredosori on the basis of function, and its use therefore leads to needless confusion.

The term may be applied to all æcidiosori, irrespective of the genera to which they belong, provided these structures consist of catenulate spores enclosed within peridia. Thus the form-genera *Roestelia, Peridermium*, and *Endophyllum* possess æcidiosori, rendering unnecessary the use of the numerous terms proposed by Arthur *et al.*, such as "cupulate æcia," "æcidioid æcia," "cornute æcia," "roestelioid æcia," "operculate æcia," "peridermioid æcia," "æcidioid uredinia," "æciotelia," and "microtelia."

Æcidiospore (pl., æcidiospores).—This term I would limit to spores produced within æcidiosori. On this account Arthur's "æciospore," and "microteliospore" of Arthur *et al.* are discarded.

Cæomosorus (pl., cæomosori).—This is suggested in place of the older "cæoma" or "cæomata," because of the reasons given under æcidiosorus, for sori of an æcidiosorial type producing catenulate spores not enclosed within peridia. Functionally æcidiosori and cæomosori are identical, but structurally the latter differ sufficiently to warrant a definite terminology, especially as they have a phylogenetic significance.

The "æcium" of Arthur and "naked æcium" or "cæomoid æcium" of Arthur *et al.* are discarded because of their ambiguity of application and inconsistency of termination.

Cæomospore (pl., cæomospores).—This is applied to a spore produced from a cæomosorus. This spore is found in literature as a "cæomospore" or "cæomatospore." Arthur's term "æciospore" has too indefinite an application to be used, as has been shown under æcidiospore.

Uredosorus (pl., uredosori).—This term has had an almost universal application since it was proposed by De Bary in 1865; and consequently is regarded (together with teleutosorus) as the standard term for a sorus. Arthur's "uredinium" is discarded, since it is not consistent with this and other terms in use. The term "æcidioid uredinia" of Arthur *et al.* applies to æcidiosori, and their "amphisporic uredinia" to uredosori in which are present amphispores in addition to normal uredospores. Their "hyphoid æcia" is a synonym for uredosori.

The term "uredosorus" is applied to sori in which the spores are borne singly on distinct pedicels, whether they are naked, enclosed within paraphyses, or within peridia. If accompanied by pycniosori, they are usually termed "primary" uredosori; if unaccompanied, then they may be termed uredosori or "secondary" uredosori. In many species two distinct types of spore forms are present, and these, too, are designated "primary" or "secondary" uredosori. As these terms are applied either on a morphological or functional basis, their use is liable to confusion. This ambiguity could be overcome by discarding the terms "primary" and "secondary" and substituting the symbols ^{I} for sori accompanied by pycniosori, ^{II} for

types of sori with spores morphologically different from the first type. Thus uredosori[i] (and uredospores[i]) would indicate these sori where accompanied by pycniosori; uredosori[ii] (and uredospores[ii]) would indicate a spore-type differing from the normal; and uredosori (and uredospores) would indicate normal sori unaccompanied by pycniosori, or sori in which no diversity of spore-type occurred.

Arthur *et al.* have proposed "stylosporic æcia" or "urediniod æcia" for uredosori[i].

Uredospore (pl., uredospores).—This term has had almost universal application since it was proposed by De Bary. As uredospore, æcidiospore, and teleutospore have become standard terms for the spore forms of the rusts, their continued use is recommended, and terms employed by Arthur regarded as unnecessary. "Stylospore" of Tulasne and "urediniospore" of Arthur are synonyms.

Teleutosorus (pl., teleutosori).—This, like uredosorus, has become a standard term for this type of sorus, being in almost universal use since it was proposed by De Bary. The German "sporelager" and Arthur's "telium" are synonyms. "Microtelium," proposed by Arthur *et al.*, cannot be used, as it was employed additionally for æcidiosori (of *Endophyllum*).

Teleutospore (pl., teleutospores).—This, like others recorded above, has had a general application since it was proposed by De Bary. "Perfect spore" of Tulasne, "probasidium" of Van Tieghem, and "teliospore" of Arthur are synonyms. "Microteliospore" of Arthur *et al.* should also be discarded, since it was applied additionally to æcidiospores (of *Endophyllum*).

Basidium (pl., basidia).—This was proposed by Brefeld for the structure produced by the germinating teleutospore, for, as he has shown, this is morphologically and functionally a true basidium. By later workers it has been applied to similar structures produced by germinating æcidiospores of species of *Endophyllum*, cæomospores of forms of *Gymnoconia Peckiana* ("*Kunkelia*" of Arthur) and uredospores of *Botryorhiza*. "Promycelium" and "probasidium" are synonyms. The term was erroneously applied by De Bary (1887, p. 274) to the æcidiospore initials.

Basidiospore (pl., basidiospores).—Proposed by Brefeld for spores produced on the basidia developed by germination of the teleutospore. "Sporidium" of Tulasne, "sporidiolum" of De Toni, and "promycelial spore" of Plowright are synonyms.

That some such revision and standardization of current terminology is necessary becomes evident when the large number of terms under discussion is considered. This may be shown graphically thus (revised terms in italics):—

Proposed Standard Term.	Terms which are more or less in General Use.*	
pycniosorus	spermogonium	pycnium (1).*
	spermagonium	pycnidium.
	spermogone.	
pycniospore	spermatium	pycniospore (1).
	conidium	pycnidiospore.
æcidiosorus	æcidium	æcium (1).
	æciotelium (3)	microtelium (2).
	cupulate æcium (2).	
	æcidioid æcium (2).	
	cornute æcium (2).	
	roestelioid æcium (2).	
	operculate æcium (2).	
	peridermioid æcium (2).	
	æcidioid uredinium (2).	

* Terms proposed by Arthur (1905) are indicated by the numeral (1); those proposed by Arthur *et al.* (2); that proposed by Arthur (Bot. Gaz., Vol. 80, pp. 219–23, 1925), (3).

Proposed Standard Term.	Terms which are more or less in General Use.	
æcidiospore	æcidiospore microteliospore (2).	æciospore (1).
cæomosorus	cæoma æcidium cæomoid æcium (2).	æcium (1). naked æcium (2).
cæomospore	cæomospore cæomatospore æcidiospore.	æciospore (1). microteliospore (2).
uredosorus	uredosorus	uredinium (1).
(uredosorus[1])	hyphoid æcium (2) uredinioid æcium (2).	stylosporic æcium (2).
uredospore	uredospore stylospore.	urediniospore (1).
(uredospore[1])	primary uredospore uredinioid æciospore (2).	stylosporic æciospore (2).
teleutosorus	teleutosorus sporenlager	telium (1). microtelium (2).
teleutospore	teleutospore probasidium	teliospore (1). microteliospore (2).
basidium	basidium promycelium.	probasidium.
basidiospore	basidiospore sporidiolum sporidiole.	sporidium. promycelial spore.

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